THE ALIMENTARY CANAL OF THE LARVA OF ALTICA BIMARGINATA SAY (Coleoptera).*

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1. THE GROSS ANATOMY OF THE LARVAL CANAL.

In the alimentary canal of the alder flea-beetle, *Altica bimarginata* Say, (Chrysomelidæ) as in insects generally, three primary divisions of the digestive tract are at once evident; the fore-intestine (stomodaeum), the mid-intestine (mesenteron or ventriculus), and the hind-intestine (proctodaeum). In this larva, the comparatively short alimentary canal, which is a nearly straight tube with few convolutions, is somewhat less than half again as long as the body. The writer has already published a figure showing the general structure (Woods 1916, Fig. 1).

The alder flea-beetle is entirely a plant feeder, living usually on the leaves of the alder (*Alnus incana* Moench), or more rarely on the willow (*Salix* spp.), or the balsam poplar (*Populus balsamifera* L.). Among adult insects the carnivorous species as a rule have rather short, straight intestines, whereas the phytophagous species tend to have longer and more convoluted digestive tracts. The larva of the alder flea-beetle does not really form an exception to this generalization, although at first sight it may appear to; for the alimentary canal, though short, is of considerable diameter throughout, so that what it may lack in length is made up in volume. Gastric coeca such as are developed in the Acridiidæ or in *Corydalis* are entirely wanting.

The fore-intestine is short, extending back only as far as the beginning of the second thoracic segment. Two divisions only are recognizable in it upon dissection, but histologically four regions can be distinguished, the first three appearing to constitute a single region macroscopically. These parts are first

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the buccal cavity, then the pharynx (the limits of which are determined by the attachment of the muscles which run from the alimentary canal to the body wall), and third, a short, narrow, muscular oesophagus which extends as far as the prothorax, where it gradually broadens out into a thin-walled distensible crop, the fourth division, the diameter of which is half as great as that of the mesenteron. A constriction, as well as a conspicuous difference in the thickness of the walls, marks externally the separation between the fore-intestine and the mid-intestine.

The mid-intestine composes by far the largest part of the digestive tract of this species. The ventriculus runs through the body as a straight tube of nearly uniform diameter, from a point near the beginning of the mesothorax to the end of the fourth abdominal segment, where a slight constriction is apparent; from here on it is somewhat convoluted and of less diameter, extending nearly or quite to the end of the seventh abdominal segment. Correlated with this macroscopic division into the two sections, is a differentiation of the lining epithelium.

The hind-intestine, which is composed of three regions, begins in the posterior portion of the seventh abdominal segment, where it joins the mid-intestine at a sharp angle. The six Malpighian vessels arise at the point of union. Their origin and distribution has already been discussed (Woods 1916). They are divisible into two series, the first (i. e., posterior) consisting of four vessels, and the second (i. e., anterior), of two. The vessels of the second series arise as separate evaginations from the intestine at the point where the mid-intestinal epithelium passes into that of the hind-intestine. The vessels of the first series unite into a bladder, which opens directly (i. e., without a stalk or urethra) into the lumen of the ileum (first division of the hind-intestine), slightly posterior to the evagination of the tubes of the second series. After a greater or less course through the body-cavity, the vessels of the first series unite into two pairs, and to each pair is joined one of the vessels of the second series, so that two common trunks of three vessels each are formed. These trunks pass into the wall of the colon (second division), where they end blindly in irregular ramifications.

At the junction of the mid-intestine with the hind-intestine, there is a sharp turn in the alimentary canal, so that, between the mesenteron which runs caudad and the ileum which runs cephalad, is formed a U-shaped bend, on the inner side of which the bladder opens. Having bent forward, the hind intestine extends as far cephalad as the posterior edge of the fifth abdominal segment, where it turns back on itself; this bend marks externally the separation between the ileum and colon. The colon, which is nearly straight, runs caudad as far as the anterior edge of the ninth abdominal segment, ventrad of the ileum. The colon passes directly into the rectum (third division), which is only one segment long. The anal opening is in the center of the anal proleg, and is shaped like an inverted Y. Macroscopically no difference is apparent between the ileum and the colon. The colon is smaller than the second division of the ventriculus; anteriorly, the colon is of the same diameter as the ileum, but it gradually increases in size posteriorly. The rectum is surrounded by powerful circular muscles, which show up clearly in a dissected specimen, and clearly differentiate it from the rest of the alimentary canal.

The structure of the different regions of the alimentary canal is discussed in the remainder of this paper. The parts are considered in order, beginning at the anterior end.

2. THE HISTOLOGICAL STRUCTURE OF THE ALIMENTARY CANAL.

The Fore Intestine.

THE MOUTH-PARTS AND THEIR MUSCLES.

Mouth parts. The mouth parts of the larva of the alder flea beetle consist of the typical biting pieces; a labrum, two mandibles, two maxillæ, and a labium. The writer has already published figures of these structures (Woods 1917, Fig. 19).

Cuticular invaginations. There are four cuticular invaginations in the head of this larva, one unpaired and three paired, which serve for the attachment of muscles. The unpaired cuticular invagination extends along the mid-dorsal line of the head from the caudal margin of the epicranium as far cephalad as the clypeus. Both primary and secondary cuticulæ are equally involved. The paired invaginations arise from the labrum, the mandibles and the maxillæ.

The first is a very slight cuticular invagination on each side of the labrum. Both cuticular layers take part in its formation. The mandibular tendon is a long chitinous invagination extending caudo-mesad from the posterior edge of the inner face of the mandible. It is formed almost entirely of the secondary cuticula. The maxillary tendon arises at the end of the chitinized portion of the stipes, and extends mesad in a curved line, so as to form a semi-circle. Both layers of chitin contribute equally to its formation.

Muscles. Two sets of muscle fibres are connected with the labrum. A large muscle fibre runs on each side from the labral invagination to the median dorsal invagination. Their contraction closes the labrum firmly against the mandibles. The second set consists of five or six fibres which run between the labral invaginations. Their contraction tends to pucker the labrum. There does not seem to be a set of fibres to open the labrum. All of these muscles are cephalad of the oral invagination, and of the supra-œsophageal ganglion.

The muscles connected with the mandibles occupy the greater part of the head cavity. There are two principal sets. Both are attached to the mandibular tendon; the flexor muscles extend to the median dorsal invagination, or to the body wall entad of the tendon, while the retractor muscles extend to the cuticula ectad of the tendon. The most cephalic fibres are anterior to the labral muscles, while others extend caudad as far as the œsophageal connectives. There is also a third set of mandibular muscles which are but slightly developed. They are inserted at one end on the cuticula of the outer face of the mandible, and at the other on the cuticula of the body wall at the base of the mandibles. Their contraction would serve to close the mandibles very tightly.

The maxillary muscles arise on the maxillary tendon and extend to the gula. There are about twenty fibres connected with each maxilla.

The labial muscles arise on the thickened cuticula at the distal end of the mentum, and are inserted on the gula. There are about five fibres on each side of the labium.

Attachment. The muscles are attached through the hypodermis to the secondary cuticula (or through the epithelium to the secondary intima) both here and elsewhere in the body.

The hypodermal cells through which the attachments are made become fibrillar, and their fibrils interlace with those of the muscles. (See figure 1, A). In some sections of just molted larvæ, these tendons are quite long, but usually the cells are not drawn out at all. (See figure 1, B). The basement membrane of the hypodermis or epithelium appears to be continuous with the sarcolemma of the muscles.

THE BUCCAL CAVITY.

As is to be expected, longitudinal sections show clearly that the cuticula of the body wall is directly continuous with the intima of the fore-intestine, the hypodermis with the epithelium, and the basement membrane of one with the basement membrane of the other. The primary cuticula is of about the same thickness as the primary intima, but it becomes deeply pigmented and beset with many cuticular nodules as soon as it is outside of the oral invagination. The secondary cuticula is also of about the same width as the secondary intima, and both stain pink with eosin. The intima of the buccal cavity is armed with small backward directed spines.

The epithelial cells are considerably larger than those of the hypodermis, but the transition is gradual and there is no abrupt change of type, the cells first becoming higher than the flat hypodermis, and then gradually broadening out into the cuboidal form characteristic of the pharyngeal and œsophageal epithelium.

THE PHARYNX.

In this species, the limits of the pharynx can be determined only by the attachment of the muscle fibres which run to the body wall. Dorsally there are two sets of these, one of four fibres running perpendicularly, and the other of three extending at an angle, to the body wall. Ventrally there is a single set which consists of two large fibres running nearly vertically to the body wall. These muscles are all paired. They are attached to the intima in the usual way, and their sarcolemmata appear continuous with the basement membrane.

The oral invagination is shown in figure 2. The location of the pharyngeal muscles is shown in figure 3.

The histological features of the pharynx and œsophagus are identical as regards the type of intima and epithelium, which are discussed under the latter region. In the pharynx the epithelium is simple and is not thrown into the folds so characteristic of the œsophagus, and this character helps to distinguish between the two regions.

THE ŒSOPHAGUS.

Intima. In this region the intima, which is comparatively well developed, appears, in cross sections, to be thrown into a series of strong longitudinal folds, usually six in number. The primary intima is well developed; the secondary intima is thicker, and stains with eosin. The primary intima bears sharp backward directed spines. The apparent teeth which the folds make almost close the lumen at the anterior end. but become weaker and weaker posteriorly.

Epithelium. The epithelium of the œsophagus is composed of large cuboidal cells; the cell divisions are not always clear, but this is doubtless due to the fixative, and does not represent any tendency toward a syncytium. There is a great variation in the size of the cells. The cytoplasm, which stains a violet-pink with eosin, appears almost homogeneous; it is non-granular and non-vacuolar. The nuclei are round-oval both in cross and longitudinal sections; they are comparatively small, and are densely filled with coarse deep-staining chromatin granules.

There is no indication of salivary cells in the œsophagus as were reported for *Hydrophilus* by Plateau (1874), and have since been recorded for several other insects.

Just after a molt, and throughout each instar, the epithelial cells lie close against the intima, and the above description has reference to such a condition. But several days before the insect is ready to cast its skin, a very characteristic premolting condition develops. The cells, which seem to be glandular in their nature, appear to secrete a fluid beneath the intima. They become fibrillar entad, and the spaces between the narrow cytoplasmic strands are probably filled with a secretion. As this process continues, in a characteristic section, the epithelium seems separated from the intima by a fibrillar vacuolar portion, which stains light blue with Delafield's hæmatoxylin. Toward the end of each instar the fibrillar portion constitutes the bulk of the apparent teeth which the folds of the intima make, and the epithelium does not pass out into these projections at all, as it does earlier in the instar. At all times, the true cytoplasmic area of the cells is sharply marked off from the fibrillar portion.

This fluid doubtless functions in connection with the molting of the intima of the fore-intestine, for this is of course shed at each molt, with the rest of the chitinous structures derived from the ectoderm.

The epithelium in the newly hatched larva, and after each of the two molts, lies directly against the intima. This fibrillar secretion is developed in all three of the larval instars. Eventually it also extends out more or less into the undifferentiated hypodermis of the body wall, with which the epithelium is continuous, but this premolting condition is always apparent in the alimentary canal before any of the hypodermal cells are affected. In the full grown larva, this area is apparent at least three or four days before it ceases feeding. The new intima appears on the last day before the larva enters the ground, and the secondary intima becomes apparent on the fourth day of prepupal life.

The œsophagus is shown in cross-section in figure 4; a few epithelial cells, in the typical state, in figure 5; a few epithelial cells in the premolt condition, in figure 6; and a few epithelial cells after the new intima has been formed, in figure 7.

Basement membrane. A structureless limiting membrane is clearly distinguishable in all of the sections which were examined. Neither here nor elsewhere in the canal has the writer found nuclei in the basement membrane, and he believes that it is formed by the hypodermal cells themselves, and is not of connective tissue.

Longitudinal muscles. From twenty to twenty-five longitudinal muscle fibres occur inside of the circular muscle layer. They are inserted proximally on the intima at the very beginning of the pharynx; they continue not only throughout the fore-intestine, but through the mid-intestine, and a part of the hind-intestine; distally they are inserted on the intima at the end of the ileum. In a general way, the arrangement of these muscles is like that described by Balbiani (1890) for *Cryptops*.

Circular muscles. The circular muscles are strongly developed. There is but a single layer of them. The most cephalic muscle is inserted on the intima at the very beginning of the pharynx, but they are lodged in a connective tissue envelope which is continuous throughout the whole alimentary canal as far as the rectum, and forms a complete membranous cylinder around the digestive tube. As is the case with all of the muscles of the alimentary canal of this insect (and probably of all others), they are clearly striated.

THE CROP.

Transition. The transition from the œsophagus to the crop is gradual. The lumen grows gradually wider, the epithelium becomes thinner and more stretched, and the chitinous folds become less and less pronounced as one traces the œsophagus posteriorly.

Intima. The intima is very much thinner than in the œsophagus, and while it is thrown into many minute wavy folds, the six large primary folds have disappeared entirely. Both primary and secondary intima may be recognized; they are of the same nature as the corresponding structures in the œsophagus, but are much more delicate.

Epithelium. In both cross and longitudinal sections, the cells appear as if they were stretched; their bases are long, and their altitude low, so that instead of being cuboidal, they present the aspect of long, narrow rectangles. The oval, granular nuclei stain quite deeply, but are not as chromatic as those in the pharyngeo-œsophageal epithelium. The cytoplasm is homogeneous, non-granular and non-vacuolar.

As in the rest of the fore-intestine, a fibrillar area is developed between the epithelium and the intima previous to each molt. It is much less extensive than in the pharynx and œsophagus, probably because the thin, little folded intima is shed much more easily than the thick, strongly folded intima which lines the other regions.

A cross-section through the crop is illustrated in figure 8.

Basement membrane. A well developed basement membrane is present.

Longitudinal muscles. The longitudinal muscles are represented by isolated striated fibres, which continue anteriorly into the pharyngeo-œsophageal region, and posteriorly into the ventriculus.

Circular muscles. The circular muscles are much stronger than the longitudinal fibres. They appear to be continuous with the muscles of the œsophagus anteriorly and with those of the ventriculus posteriorly, since they all lie in the same connective tissue sheath.

THE ŒSOPHAGEAL VALVE.

In typical cases among insects, such as *Pieris* or *Simulium*, the œsophageal valve is a large fold of the fore-intestine, which projects down into the mid-intestine, almost closing the aperture between them. The function assigned to it is that of preventing the regurgitation of food, due to the peristaltic movements of the intestine.

In *Altica bimarginata* there is a fold of the fore-intestine which projects slightly down into the mid-intestine, and marks the point of transition between these two regions. It is by no means large enough to close the lumen and can be of but little if any use as a means of preventing the repassing of food into the fore-intestine. However, there is a strong constriction between the crop and the ventriculus, and the opening between the two is much less than the diameter of the alimentary canal at this point, so an œsophageal valve is little needed, and this fold is probably all that is necessary. In its structure the œsophageal valve is much like the rest of the crop. Intima, epithelium and basement membrane are clearly distinguishable. The primary intima becomes very thin, but distinction between primary and secondary intima continues to the end. This condition is very similar to that described by Poyarkoff (1910) in the elm leaf beetle.

The œsophageal valve of *Altica bimarginata* is shown in figure 9.

THE TRANSITION BETWEEN THE FORE-INTESTINE AND THE MID-INTESTINE.

Intima. The intima disappears at the end of the fore-intestine.

Striated border. A striated border is developed on the inner face of the cells in place of an intima throughout the mid-intestine.

Epithelium. There is a well marked transition between the type of epithelium characteristic of the fore-intestine and that characteristic of the mid-intestine, even though there is no sudden change. The cells of the fore-intestine at the posterior face of the œsophageal valve become first cuboidal, and then narrower and more elongate, passing almost imperceptibly into the type characteristic of the mid-intestine.

The transition area is shown in figure 9.

Basement membrane. The basement membrane is continuous from the crop to the ventriculus.

Imaginal ring. There is no clearly defined imaginal ring. The cells on the extreme posterior face of the œsophageal valve are very small and close together, and probably constitute the imaginal ring of the fore-intestine. This is very comparable to the conditions described by Poyarkoff (1909, 1910) in the elm leaf beetle, where the imaginal mid-intestine is derived from the cells of the posterior face of the larval œsophageal valve, although these cells are not sharply separated off as a distinct imaginal ring in the larva. The cells are never crowded together in *Altica* so as to form an apparently several layered imaginal ring, as in the case in Cybister (Deegener 1904), where the ring lies above the œsophageal valve.

Longitudinal muscles. The longitudinal muscle fibres are continuous from the fore-intestine into the mid-intestine. With respect to the connective tissue sheath in which the circular muscles lie, they are internal in the fore-intestine, but at the point of junction between the crop and the ventriculus, each fibre divides into two or three smaller ones which penetrate this sheath, so that the longitudinal muscles lie outermost in the mid-intestine. There are about twenty of these fibres in the fore-intestine, and about forty at the anterior end of the mid-intestine.

The passage of these muscles from the crop to the ventriculus is shown in figure 10.

Circular muscles. The circular muscles of the fore-intestine and the mid-intestine appear to be continuous, since they both lie in the same connective tissue tube around the intestine, but doubtless here, as in all insects in which the conditions have been studied, embryologically they have very different origins, and are not homologous. The muscles immediately at the junction form a strong sphincter.

The Mid-Intestine.

THE FIRST DIVISION OF THE VENTRICULUS.

Striated border. The epithelium of the mid-intestine never supports an intima in insects, but instead is clothed with a striated border, which is very characteristic of this region. This striated border is usually considered as a vestige of a formerly ciliated condition. In this species, the striated border is always conspicuous and well developed. The striæ are close together, and are not always sharply separated from the cytoplasm interiorly.

Epithelium. The epithelium is of the columnar type, and the cells are very clearly defined. They vary greatly in size and shape; they may be almost cuboidal, or more than twice as high as wide, probably depending upon their physiological condition. In general, the more anterior cells are the higher. The nuclei are large, median, and almost round; they are quite densely filled with coarse chromatin granules, and there are from one to three larger granules, probably nucleoli. The cytoplasm is non-granular, but is usually more or less vacuolar.

The secretion is merocrine. In the resting state the cytoplasm becomes charged with vacuoles, which pass to the outer margin of the cell, beneath the striated border, where they merge into larger drops. At the time of the secretion these cytoplasmic balls pass out of the cell through the striated border, apparently pushing away the striæ on either side. In the process of being discharged, they remain more or less attenuated on the inner end, but they become spherical as soon as they are free in the lumen of the canal. They stain with eosin, and appear homogeneous.

The first division of the mid-intestine is shown in figure 11.

Replacement cells. During the pupal and prepupal period of most, if not all, insects, the epithelium of the mid-intestine breaks down completely, and a new epithelium is built up from little cells or groups of cells, which lie at the base of the ordinary epithelial cells. In *Altica bimarginata* at least, they seem to remain quiescent during larval life, but begin to proliferate actively during the prepupal period, in which the old larval epithelium breaks down, and a new epithelium is developed, apparently out of these replacement cells. They are apparent in sections through larvæ which have just hatched from the egg.

The replacement cells are more or less triangular cells, which lie at the bases of the functional cells, at irregular intervals, wedged in between two of the cells. The nucleus is large in proportion (it is almost as large as that of the active cells), and there is but relatively little cytoplasm, which is non-granular and non-vacuolar. The nuclei stain a little more deeply, and the particles of chromatin are a little coarser than is the case with the nuclei of the functional cells. Three replacement cells are shown in figure 11.

Basement membrane. A very delicate basement membrane, on which both the functional and the replacement cells rest, can be detected in well fixed preparations and is doubtless present in all cases.

Circular muscles. Striated circular muscle fibres surround the mid-intestine, lodged in a continuous sheath of connective tissue, which forms a complete tube around the canal. The fibres are branched, and often interlace.

Longitudinal muscles. The longitudinal muscle fibres lie outside the circular muscle layer. There are about forty of these fibres, which branch and interlace to some extent.

THE SECOND DIVISION OF THE VENTRICULUS.

Striated border. The striated border is not well developed in this region, but is doubtless always at least feebly developed, even when it is not apparent in sections. It is not even as sharply separated from the cytoplasm as in the preceding region.

Epithelium. The columnar epithelium is composed of cells which are comparatively much longer and more slender than those of the preceeding region. On the free end the cell outlines are less even and very irregular, instead of about equal and straight. The nuclei are of about the same size, but are oval rather than round; they are median, or slightly basal if the secretion be abundant.

The second division of the ventriculus is shown in figure 12.

The secretion takes place in the same manner as before, but much more actively and abundantly. It is of quite a different chemical nature, for the cytoplasmic balls stain a light pink with eosin, and are very granular.

Replacement cells. The replacement cells are of the same type and arrangement as in the preceding region.

Basement membrane. The basement membrane is of the same character as in the preceding region.

Circular muscles. The condition of the circular muscle fibres is the same as in the preceding region.

Longitudinal muscles. The longitudinal muscle fibres are continuous with those of the preceding region. They are more numerous, as the fibres split up more or less at the point of junction between the two regions.

The musculature of the two regions of the ventriculus is shown in figure 13.

The Hind Intestine.

THE TRANSITION BETWEEN THE MID-INTESTINE AND THE HIND-INTESTINE.

Striated border. The striated border stops with the end of the mid-intestinal epithelium. It is very faint and feebly developed, as is characteristic of the whole posterior portion of the second division of the ventriculus.

Intima. A chitinous intima originates with the epithelium of the hind-intestine. The primary intima is very thin, the secondary somewhat broader. Neither layer is stained by eosin nor by Delafield's hæmatoxylin.

Epithelium. There is a sharp break between the epithelium of the mid-intestine and that of the hind-intestine. The epithelial cells of the mid-intestine do not differ markedly from the normal as the transition area is approached, save that the replacement cells become very numerous, and tend to form small nests or nidi, instead of occurring singly. At the extreme end of the mid-intestine, the cells lose their columnar character, the cell divisions become very indistinct, and the replacement cells are abundant. The epithelium of the hind-intestine is clearly separated from that of the mid-intestine. The cells, at first narrow, become higher and wider, and shortly merge into an epithelium perfectly typical of the proximal division of the ileum. The cytoplasm is vacuolar and very fibrillar.

The transition area is shown in figure 14.

Pyloric valve. There is no pyloric valve.

Imaginal ring. The cells at the extreme anterior end of the hind-intestine are very small, narrow, and pressed closely together; they probably constitute the imaginal ring of the hind-intestine, although they never present a several layered appearance. This is much the same condition which Poyarkoff (1910) described for *Galerucella.*

Basement membrane. The basement membrane of one region is continuous with that of the other.

Circular muscles. The connective tissue sheet, in which the circular muscle fibres lie, is continuous from the mid-intestine into the hind-intestine, so that the circular muscles of the two regions appear to be homologous and continuous but doubtless embryological researches would show that, as is the case with insects generally, they have entirely different origins. There is a sphincter at the point of junction.

Longitudinal muscles. The longitudinal muscle fibres are continuous from the mid-intestine into the hind-intestine. As the transition area is neared, the numerous longitudinal muscles of the mid-intestine (fifty or sixty in number) come together so as to form eighteen or twenty larger fibres, which again penetrate through the connective tissue sheath of the circular muscles, so as to lie outside of them, as is the case in the fore-intestine.

This condition is illustrated in figure 15.

THE EVAGINATION OF THE SECOND SERIES OF MALPIGHIAN VESSELS.

(It seems illogical to speak of the more anterior set of Malpighian tubes as the second series, but the writer prefers this usage, because he believes that the close association of this series with the mid-intestinal epithelium is entirely secondary, and that the opening of the bladder formed by the vessels of the first series represents more nearly the primitive insertion of the tubes).

The two Malpighian vessels of the second series arise at the extreme posterior end of the ventriculus, appearing abruptly, before there is any change in the mid-intestinal epithelium. Their cells are, however, very distinct from the ventricular epithelium. They are lined by a very faint striated border. The lumen of the vessels is continuous with that of the intestine. The two vessels arise very close together. As soon as they penetrate the connective tissue layer in which the muscles are imbedded, it continues around them as a nucleated peritoneum. Their basement membrane is continuous with that of the alimentary epithelium.

The evagination of these vessels is shown in figure 16.

Their structure and relations make it perfectly clear that any connection which they have with the mid-intestine is entirely secondary. Although there may be two or three cells of the mesenteron which lie between them and the hind-intestine, their complete fusion distally with the vessels of the first series, makes it clear that they are appendages of the hind-intestine; and their present point of origin from the ventriculus is due to secondary migration.

THE PROXIMAL PORTION OF THE ILEUM.

Proximal and distal ileum. The first division of the hind-intestine, the ileum, may be divided histologically into a proximal and a distal portion. The proximal portion extends from the beginning of the hind-intestine as far as the opening of the bladder. The distal region includes all of the ileum beyond this point.

The proximal ileum corresponds to the first region of the hind-intestine, and the distal ileum to the second region, as Poyarkoff (1910) considered them in *Galerucella*.

Intima. The primary intima is very thin, but the secondary intima is fairly thick. Neither layer is stained with eosin nor Delafield's haematoxylin, but the primary layer contains brown pigment.

Epithelium. The epithelium is composed of wide, flat cells, very much smaller than those of the distal region, as are also the round chromatic nuclei, full of densely-packed coarse granules. The cytoplasm is homogeneous, and usually non-vacular. The epithelium is thrown into small, wavy, pointed folds.

Basement membrane. The basement membrane is well developed.

Longitudinal muscles. There are about twenty longitudinal muscle fibres, which lie in a continuous connective tissue sheath. Anteriorly they are continuous with the muscles of the ventriculus, and posteriorly they are inserted on the intima at the end of the distal portion of the ileum.

Circular muscles. The circular muscle fibres are well developed and lie in the connective tissue sheath outside that of the longitudinal fibres, this sheath being continuous with that of the mid-intestine. There are thus in the ileum two connective tissue sheaths around the canal outside the basement membrane of the epithelium.

FORMATION AND ATTACHMENT OF THE BLADDER.

The four Malpighian vessels (those of the first series) whose fusion at their proximal ends is to form the bladder, run closely parallel to one another between the ventriculus and the ileum, for some little distance before they unite. At the point of fusion there is at first no change in the character of the cells, and an ovoid swelling is formed without any interruption of the separate lumen of each tube. The two outer vessels (i. e., the two nearest the ileum) unite first, and their combined lumen is lined with very small epithelial cells, with a faint striated border. The other two vessels are arranged at right angles to them, with their lumina still distinct, and their cells of the usual size. Here as elsewhere the whole enlargement is invested with a basement membrane and a nucleated peritoneum distinct from the former. The cells of the two inner vessels become smaller abruptly, and in a few sections of six micra each, an uniform bladder results, with a common lumen (made up of the fused lumina of the four vessels) lined by a single layer of epithelial cells. The striated border, faint everywhere in the fusing vessels, has now disappeared and is replaced by a thin intima. In some cases the epithelium seems to consist of more than a single layer, but this is only apparent, not real, and is due to folding. The cell divisions are never clearly distinct. The nuclei of the bladder cells are of the same essential structure throughout, although they vary greatly in size, according to the size of the cells. They are round in the larger cells, and ovoid or oval in the smaller. They are densely chromatic and stain intensely; the chromatin is in the form of coarse granules with a few larger periferal granules in each nucleus.

As the bladder approaches the ventriculo-iliac bend, the circular muscles of the intestine grow out and surround it, and the lumen of the bladder soon opens directly into that of the proximal portion of the ileum. The intima of the bladder, both primary and secondary, is directly continuous with that of the ileum and, like the latter, it does not stain either with eosin or Delafield's hæmatoxylin; the intima in the bladder is somewhat thinner, and the primary intima is not pigmented. The epithelium of the two portions is continuous; the cells of the ileum are more elongate than those of the bladder, but the nuclei are of about the same size. The basement membrane is continuous. The peritoneum, which ends when the circular muscles grow out and surround the bladder, is continuous with the connective tissue sheath in which they are lodged.

There is no suggestion of an urethra, or stalk, leading from the bladder to the intestine, such as is often present, except that two of the undulatory folds of the iliac epithelium are larger where the bladder empties, and make a sort of passageway between the two lumina. Since such a stalk is present at least in *A. nemorum* (Schindler 1878; p. 631), this may represent the first step in the development of one.

The fusion of the four vessels is shown in figure 17; the fusion of the lumina of the two outer vessels, in figure 18; the complete bladder, in figure 19; and the junction of the bladder and ileum, in figure 20.

THE DISTAL PORTION OF THE ILEUM.

Transition. As soon as the bladder has emptied into the canal, the intima is gradually reduced in thickness, and the epithelial cells become thicker, with the folds larger and less acute; the nuclei also become larger, and the cytoplasm tends to become differentiated into two regions, as is explained below. This transition is gradual, not abrupt. All of the layers of the proximal portion of the ileum are continuous with those of the distal.

Intima. The intima is divided into a primary and a secondary intima, but the latter is much thinner than in the proximal portion. It becomes progressively narrower throughout this region.

Epithelium. The epithelium is composed of large, irregularly cuboidal cells, whose boundaries are frequently so indistinct that they form an apparent syncytium. In most cases there are two areas of cytoplasm clearly distinguishable: an inner (toward the basement membrane) layer, denser and darker, staining violet-pink with eosin, and an outer, more or less fibrillar, staining light pink. These areas are of about equal width. This condition (which is doubtless related to the absorption of food, since such a differentiation is not apparent unless there is food in the intestine) is most prominent proximally, but becomes less and less distinct, although it is still plainly discernible through the whole course of the ileum. The nuclei, which are quite large, may be either round or oval; they are densely chromatic, especially around the perifery and in the center. The chromatin is present in the form of coarse granules.

In some sections the epithelium appears only slightly, if at all, folded, but usually it is conspicuously and strongly thrown into tooth-like projections, typically six in number.

The distal portion of the ileum is shown in figure 21.

Basement membrane. The basement membrane is thin, but clearly distinguishable.

Longitudinal muscles. The longitudinal muscle fibres are continuous anteriorly with those of the proximal portion of the ileum, and are inserted posteriorly on the intima at the extreme end of this region. The longitudinal muscles are continuous nearly the whole length of the alimentary canal; they arise at the extreme anterior end of the pharynx and lie inside of the circular muscle sheath in the fore-intestine; they pass outside this sheath, and are external in the mid-intestine; they pass inside again at the beginning of the hind-intestine, so that they are internal, and are finally inserted on intima at the posterior end of the ileum.

Circular muscles. The striated circular muscle fibres are well developed. They lie in a connective tissue sheath continuous anteriorly with that of the proximal portion of the ileum, and posteriorly with that of the colon.

THE COLON.

Transition. The epithelium changes gradually in type between this region and the preceding. The intima, basement membrane, and circular muscles are also continuous. The longitudinal muscles of the ileum disappear, as they are inserted on the intima at the end of the ileum, and a new layer of much larger longitudinal muscle fibres, external and not internal, appears, inserted on the intima at the beginning of this region.

Intima. The intima is slightly thicker than it was in the ileum; like the latter, it is differentiated into a primary and a secondary intima, the former being very thin.

Epithelium. At the point of union between the colon and the ileum, the epithelial cells of one region closely resemble those of the other. The intestine bends again caudad at the junction, and a section through this region shows at one side typical ileum cells and at the other typical colon cells, while between them are transition cells which might be assigned to either region. The cells of the ileum nearly always show a differentiation into two areas of cytoplasm, while the cytoplasm of the colon cells is only rarely so differentiated, this differentiation usually disappearing in the intervening transitional cells. There is at this point no difference in the size of the cells.

As one traces the course of the colon toward the rectum, the cells of the epithelium become flatter and flatter, this tendency beginning with the association of the Malpighian vessels with the wall of the canal. Typically, the epithelium of the colon is only about one-half as high as that of the ileum, though the cells are nearly if not quite as wide. The cytoplasm is usually of the same structure throughout, resembling the inner layer of the ileum, but rarely it is feebly differentiated into two layers as is the case in the ileum.

The nuclei are of about the same size and shape as in the preceding region, but the chromatin granules are slightly larger. Here, too, the cell divisions are obscure, probably in part at least due to the fixation. The epithelium may be unfolded, or may be thrown into six or more prominent tooth-like folds, which project into the lumen.

A typical cross-section through the colon is shown in figure 25.

Basement membrane. The basement membrane is always clearly defined.

Circular muscles. The layer of circular muscles, which is continuous with that of the ileum, is strongly developed in the anterior portion of the colon, but the fibres become weaker and weaker as one traces them caudad, although they do not disappear completely until the end of this region. The most posterior muscle is inserted on the intima of the colon, on an apodeme-like projection between the colon and rectum. Like the other circular muscle fibres, they lie in a connective tissue sheath. This sheath forms a continuous tube around the alimentary canal from the anterior end of the pharynx through the posterior end of the colon.

Longitudinal muscles. New and very strong longitudinal muscle fibres appear with the colon. They lie outside the circular muscles, not inside like the longitudinal muscles of the ileum. They begin at the point where sections through the ileo-colonic bend first show signs of the approaching constriction and separation. At their origin, they are inserted on the intima of this region. There are six of these longitudinal muscle fibres, arranged quite regularly in a typical cross section. Three of these muscles appear on the outer (left) side as soon as there is any sign of the constriction referred to above, and three are developed on the inner (right) as soon as the colon and ileum have separated. These muscles grow gradually smaller and are inserted on the intima slightly anterior to the end of the colon.

Peritoneum and Malpighian vessels. The distal ends of the Malpighian vessels are closely associated with the walls of the colon. The fusion of the Malpighian vessels into two common trunks at the end of their "coelomic" course has been pointed out already (page 298). Each trunk applies itself closely to the wall of the colon, one dorsally and one ventrally, each lying between two of the longitudinal fibres; they join the canal as soon as these fibres have been developed. As soon as the vessels have become appressed to the wall of the colon, their peritoneal sheaths grow out and join, so that a continuous peritoneal coat is formed, which completely surrounds the colon, and encloses the six muscle fibres and the two Malpighian trunks.

As soon as this tunic is complete, or even before, each trunk (which is not larger than an ordinary Malpighian tube) redivides into three vessels, which almost immediately begin to "migrate" outside the muscle fibres, so as to lie alternately with them. This "slipping" or "migration" extends through about twenty sections of six micra each before it is completed. The condition which results characterizes the greater part of the colon, and in a typical cross-section, one will find lying outside the circular muscles, a layer composed of the six longitudinal muscle fibres, alternating with the six Malpighian vessels, the whole surrounded by a nucleated peritoneum, which is a double layer, since it represents the investing sheath of the vessels. The two sheets separate at the vessels, one layer passing inside and the other outside of the tubes, but both sheets pass outside of the longitudinal muscles.

Normally the two trunks do not join the colon opposite one another as would be expected; at least, this is the case in every series which the writer has examined. The ventral trunk occupies what may be termed the normal position, and when it redivides into three vessels, the central vessel remains in position and each of the two lateral ones migrates around the adjacent muscle fibre. The dorsal trunk, however, does not enter exactly opposite (i. e., with three muscles intervening), but slightly to one side of the canal (i. e., with but two muscles intervening). Therefore when it redivides, it is the innermost vessel which remains in place; the outermost not only must slip outside the adjacent muscle fibre, but must also pass the next one beyond, so that in its migration it slips outside of two muscles before it is in position; the middle vessel slips outside a single fibre, the one originally adjacent to the outermost vessel, and then it is in place. Thus is brought about the regular alternation of muscle fibre and Malpighian vessels, which obtained in every instance which the writer has observed.

In the anterior part of the colon the cross-sections of the Malpighian vessels and of the longitudinal muscles are about equal in diameter. But as they pass caudad, the Malpighian vessels gradually increase in size, while the longitudinal muscles become weaker, and two-thirds caudad the Malpighian tubes are twice as large as the muscles. At this point the longitudinal muscles begin to diminish in size rapidly, and become very small, although they persist faintly to the end of the region. The circular muscles also decrease so markedly in size as to be almost negligible. The Malpighian vessels, which have been almost circular in cross-sections, now become elongated along the diameter perpendicular to the axis of the canal, and tend to crowd the longitudinal muscles inside. This tendency becomes more and more pronounced, and a little distance before the end of the colon the intestine is surrounded by a practically continuous layer of Malpighian tubes, with the small longitudinal muscles intercalated between them. The vessels do not extend along the wall of the rectum, but terminate blindly at the extreme posterior end of the colon.

It is very difficult to make out the exact course of the vessels in the wall of the colon. They seem to extend posteriorly as six parallel tubes, at first of slight diameter and almost straight, but as the diameter increases, they become more and more wavy, with larger and larger folds. It is this character which makes the tubes appear so elongate in cross-section. Toward the end of the colon, these undulatory folds are so large that those of one series almost touch those of the adjacent series, and thus they almost completely surround the wall of the colon. The vessels seem to branch irregularly, the tubes terminating blindly and separately in irregular ramifications, just anterior to the strong circular muscles which appear abruptly, and mark externally the beginning of the rectum.

The writer has already figured the course of the vessels in the wall of the colon (Woods, 1916, figure 4); and a series of cross-sections of the colon showing the different conditions described above is illustrated in figures 22–27.

THE RECTUM.

Transition. The transition between the colon and the rectum is the most abrupt in the whole course of the alimentary canal. The Malpighian vessels and the peritoneal sheath disappear abruptly, and new circular muscles make their appearance suddenly. The epithelial cells of the colon become flatter and flatter, and the cell boundaries more and more distinct near the rectum, but the type changes quite abruptly to the glandular and eosinophile cells characteristic of the rectum.

Intima. At first there are only minute wavy folds in the intima and epithelium, but posteriorly these folds become gradually more and more pronounced, and more and more tooth-like in appearance, while the lumen becomes smaller and smaller. The typical number of these "teeth" is probably six, but they are far from regular, and there may be from five to eight. As is to be expected, the primary and secondary intima are continuous with the primary and secondary cuticula respectively, of the body wall. There is no pigment in the primary cuticula for a considerable distance beyond the rectal invagination.

At the proximal end of the rectum there is a pronounced outpushing of the intima into the body-cavity; this serves as a place for the attachment of the circular muscles of the colon, and the origin of the circular muscles of the rectum.

Epithelium. The cells of the epithelium are much smaller than those in the two sections immediately preceding the rectum, and the cell divisions are much clearer. At the bases of the chitinous folds referred to above, the epithelial cells are thin and stretched out, but at the apices they are broadened out and glandular in appearance. Because the cells are so thin at their bases, they might readily be overlooked, and this probably accounts for the fact that some writers have described the epithelium as wanting in the case of similar structures. It is, of course, evident that where there is an intima there must be underlying cells to secrete it. The cytoplasm of these cells stains deep pink with eosin, and is smooth, non-granular. The nuclei are smaller than those of the ileum and colon, and are not so chromatic. Posteriorly, the epithelium becomes more and more glandular in appearance, and these gland-like cells persist out into the otherwise unmodified hypodermis of the body-wall, with which this layer is of course continuous.

The epithelial cells elaborate a "molting-fluid" exactly as was described in the case of the fore-intestine. In larvæ fixed just after a molt, or at the time of hatching, the cells of the epithelium lie close against the intima; but they begin to secrete a fluid very soon, and in a few days there is a fibrillar-vacuolar area, which stains blue with Delafield's hæmatoxylin, separating the intima and epithelium. This fibrillar area is always clearly marked off from the true cytoplasmic cellular portion. The presence of this fibrillar portion is characteristic of the rectum, and is developed in all of the instars. The new cuticula is formed ectad of this area just before each molt. The new intima is formed not more than a day before the larva enters the ground, and the secondary intima becomes apparent on the fourth day of prepupal life. The fibrillar area extends out beyond the proctodeal invagination between the hypodermis and the cuticula in the body-wall, about to the point where pigment appears in the primary cuticula, and glandular cells of a type continuous with those of the rectum do not appear in the hypodermis beyond this point.

This fluid secreted doubtless serves as an aid in molting, as was suggested under the discussion of the œsophagus, for the intima of the whole hind-intestine, like that of the fore-intestine, is shed at each molt. This fluid is developed along the whole course of the fore-intestine, but is present only in the last division of the hind-intestine. This may be due to the fact that the rest of the hind-intestine is the principal seat of absorption; the intima is much thinner, and probably slips off more easily.

A cross-section through the rectum is shown in figure 28; the rectal epithelium after a molt, in figure 29; the rectal epithelium with the fibrillar area developing, in figure 30; the rectal epithelium after the formation of the pupal intima, in figure 31; and the rectal invagination, in figure 32.

Basement membrane. The basement membrane, which is clear and well developed throughout this region, is continuous with that of the body wall.

Circular muscles. There are three distinct layers of very strong circular muscles in the rectum, each layer forming a complete ring around the alimentary canal. They have their origin on the posterior face of the apodeme-like projection from the intima at the anterior end of the rectum, and are inserted on the cuticula around the proctodeal invagination. Each layer originates and is inserted independently.

Longitudinal muscles. Longitudinal muscles are entirely lacking in the rectum.

3. THE MALPIGHIAN VESSELS.

The General Course of the Vessels.

From a morphological point of view, the Malpighian vessels of an insect are ectodermal structures which arise during embryonic life as evaginations of the distal end of the hind-intestine. In the larva of the alder flea-beetle, they are six in number, constituting two series of four vessels and two vessels respectively. The details of their course in the body cavity has already been pointed out (Woods, 1916), and their relation to the colon is discussed elsewhere in this paper (pages 298–302). It should be clearly understood that they do not open into the colon, and that their only connection with the lumen of the alimentary canal is at the point of their evagination.

We may summarize the distribution of the tubes in the larva as follows (beginning at the distal end): Six Malpighian vessels extend parallel to one another, running cephalad in the wall of the colon; they unite at the anterior end of this region to form two common trunks, which, leaving the wall of the intestine, split up into a single tube, and a common stem representing a pair of tubes; the single tube, which is very short and delicate, runs directly to the ventriculus, where it is inserted isolated into the wall of the intestine, just at the point where the mid-intestine joins the hind-intestine; each common stem soon splits up into two vessels, which have a long course through the body-cavity, but eventually all four unite to form a single common urinary bladder, which empties directly into the ileum, at a point a little posterior to the insertion of the two shorter tubes.

For convenience in discussing the histological structure of the tubes, the writer has spoken of that portion of the Malpighian vessels enclosed in the walls of the colon, as the "included" portion, and the part which lies free in the body cavity as the " 'coelomic' " portion. This is of course a very free use of the term, for the coelome, or true body-cavity, is very much reduced in insects, and the apparent body-cavity is in reality only a greatly enlarged haemocoele, or blood sinus.

The Histological Structure of the Vessels of the First Series.

the "coelomic" portion.

Proximal. Interiorly, the epithelial cells of the proximal portion of the Malpighian tubes of the larva are covered by a wide, lightly staining striated border, composed of many very fine and closely appressed striæ, beneath which is a narrow band of dense deeply-staining cytoplasm. The cell cytoplasm, which stains deep violet-pink with eosin, is very granular, and presents a more or less fibrillar aspect. The nucleus, which is proportionately large, varies in shape from elliptical to circular, and is typically basal in position. The chromatin granules are larger than those of the distal nuclei and are not so densely compacted. They occur especially around the perifery.

Vacuoles in these cells indicate a secretory activity, but the writer has not followed the secretion cycle. From the sections studied it would appear that tiny secretion vacuoles are formed between the nucleus and the basement membrane, which then migrate around the nucleus so as to lie between it and the striated border, where they fuse to form a large secretion vacuole at the tip, which causes the cell to bulge out, papilla-like, into the lumen of the tube.

The epithelial cells have a very delicate but distinct basement membrane, besides a nucleated peritoneal sheath which completely surrounds the vessels.

There is no indication of a lightly staining fibrillar area just inside of the basement membrane, as is the case in the cells of the distal portion.

Distal. The epithelial cells of the distal region of the vessels are larger than those of the proximal region and the striated border is extremely delicate. The cytoplasm stains deeply with eosin, usually a little more intensely than in the cells of the proximal portion. There is a narrow area of light fibrillar cytoplasm (which even under an oil-immersion lens looks not unlike the striated border) just within the basement membrane which here too, though delicate, is clearly distinct from the nucleated peritoneum. The rest of the cytoplasm is homogeneous, and stains intensely. There may be few or several vacuolated areas in the cells, just interior to the narrow band of dense cytoplasm, lying just inside the fibrillar area referred to above.

The nucleoplasm stains a light violet with Delafield's haematoxylin, while the coarse irregularly scattered, but densely compacted chromatin granules stain deep violet. One or two chromatic granules are usually larger than the others. The oval nuclei are of about the same size as those in the proximal portion.

Typical. In a typical cross section through one of the vessels of the first series of larval tubes there are four cells, usually not more than one or two of which will be cut through the nuclei. The nuclei are oval, large and central in position. The chromatin granules are large, rather sparse and mostly periferal.

The lumen is lined by a very narrow lightly stained striated border of very closely set striæ. Between this border and the basement membrane, four areas of cytoplasm may be distinguished, the last two very narrow and the first two of about equal width. The first area is composed of more or less reticular cytoplasm which stains deeply with eosin. The second area is made up of lighter staining, homogeneous cytoplasm, surrounding secretion vacuoles. The third area is a very narrow band of dense, intensely-stained cytoplasm. The fourth area stains lightly, and is fibrillar, seemingly composed of very fine and closely apposed striations. Outside of this area is the very delicate basement membrane and the whole tube is surrounded by a nucleated peritoneum.

The aspect of the tubes varies greatly according to the fixing fluid used, and according to the stage of secretion. The differences between the proximal and distal portions of the tubes may be exaggerated in the above account, for they do not always seem to be so well marked, but in all cases which the writer has observed, the cells of the two regions present a different microscopical aspect, and the striated border seems always to be well developed in one and almost wanting in the other. This character agrees with the description of the tubes of *Scaurus* (Tenebrionidæ), by Leger and Hagenmuller (1899), where the proximal end of the vessels is lined with conspicuous cilia, but no cilia can be detected in the distal end.

All of the cells of the "coelomic" portion agree in that they undergo cyclic changes, denoting secretory activity. The cycle is probably the same in all of the cells. While the writer has not made a careful study of the process, it seems to be approximately as follows: The nuclei of the cells at first lie nearer the lumen than the basement membrane; vacuoles are formed between the nucleus and the basement membrane, which pass around the nucleus and lie between it and the striated border; the cell then bulges out, papilla-like, into the lumen as these small vacuoles fuse into one large one, which finally discharges its contents into the lumen of the vessel.

THE COMMON STEM.

The cells of the common stem formed after the vessels have fused in pairs, as well as those of the common trunk formed by the union of the three vessels, do not differ in appearance from those of the distal region of the vessels, as described above, except that the writer has not been able to detect any trace of the striated border.

The Histological Structure of the Vessels of the Second Series.

The cells of the second series of tubes are considerably smaller than those of the first series, and the nuclei, which are round or oval, are much smaller. The nuclei are densely chromatic; the chromatin granules are of the same color and size as those in the nuclei of the first series. The cytoplasm stains less intensely with eosin and is pinkish rather than purple-pink. The lumen is very slight. There is a distinct basement membrane and a nucleated peritoneum.

The Vessels in the Wall of the Colon.

Both cells and nuclei of the vessels in the wall of the colon are very much smaller even than those of the second series. The nuclei, which are proportionately large, are round or oval, and densely chromatic, with small dark-stained chromatin granules. The cytoplasm is homogeneous, and is not divided into areas; it stains less intensely with eosin than that of the free portion of the tubes. The writer has not been able to find any trace of a striated border lining the lumen. There is a very delicate but distinct basement membrane, and a nucleated peritoneum.

4. THE SALIVARY GLANDS OF THE LARVA.

The salivary glands of insects are not appendages of the alimentary canal, but are independent ectodermal invaginations, which open secondarily, if at all, into the mouth cavity. In the larva of the alder flea-beetle there is a single pair of these glands, more properly in this case to be called maxillary glands, which open at the inner base of the maxillæ. They are simple tubular glands, short, lying entirely within the head, usually extending along the ventral side nearly to the thoracic border, and then bending up at a sharp angle, running nearly to the dorsal body wall.

Sections through the invagination of these tubes (see figure 33) show that the chitin of the central duct (which is differentiated into a primary and a secondary layer) is continuous with the cuticula of the body wall. There is no transition between the hypodermis and the gland cells, but the glandular epithelium is developed abruptly, as soon as the invagination takes place; it is of course continuous with the perfectly unmodified hypodermis just outside.

In cross and longitudinal sections alike, it is clearly to be seen that the glands are composed of a single layer of cells around a common central duct. This chitinous duct is always clear in all of the sections which the writer has examined. The cells are large, and of the cuboidal epithelium type. The nuclei are proportionately large. round or oval, and densely chromatic; the chromatin is in the form of fine granules, except for four or five coarser granules in each nucleus. The position of the nuclei is variable, but usually they are median, or nearer the duct. The cytoplasm is reticular, and seems to consist of a fine net-work. Large vacuoles may appear in the cells, depending on the state of secretory activity.

There is a delicate limiting membrane outside, which is continuous with the basement membrane of the hypodermis.

The labial glands, which constitute the prominent salivary glands, or cephalic silk glands, of the Lepidoptera and Trichoptera, for example, are entirely absent in the larva of the alder flea-beetle, as in insects of this order generally, both larvæ and adults.

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Since so many good bibliographies of the papers dealing with the alimentary canals of insects are available the writer has included here only those papers to which actual reference has been made in the preceding discussion.

EXPLANATION OF PLATES.

Plate XXVI.

Fig. 1. Diagrams to show the attachment of muscles to the cuticula; A, the normal condition; B, after a molt, showing the tendons.
Fig. 2. The oral invagination. longitudinal section.
Fig. 3. The musculature of the pharynx (longitudinal section).
Fig. 4. The oesophagus. cross-section.
Fig. 5. The oesophageal epithelium, normal condition.
Fig. 6. The oesophageal epithelium, premolt condition.
Fig. 7. The oesophageal epithelium, after the formation of the new intima.
Fig. 8. A portion of the crop, cross-section.
Fig. 9. The oesophageal valve, and the transition from the fore-intestine to the mid-intestine (longitudinal section).
Fig. 10. The transition in the musculature from the fore-intestine to the mid-intestine.
Fig. 11. A portion of the first division of the ventriculus, cross-section.
Fig. 12. A portion of the second division of the ventriculus, cross-section.

Plate XXVII.

Fig. 13. The musculature of the mid-intestine, showing the transition from the first division of the ventriculus to the second. (The constriction marks the point of separation between the two divisions).
Fig. 14. The transition from the mid-intestine to the hind-intestine (longitudinal section).
Fig. 15. The transition in the musculature from the mid-intestine to the hind-intestine.
Fig. 16. The evagination of the second series of Malpighian vessels.
Fig. 17. The first stage in the formation of the bladder; the fusion of the four Malpighian vessels of the first series.
Fig. 18. The second stage in the formation of the bladder; the fusion of the lumina of the two outer vessels.
Fig. 19. The completed bladder.
Fig. 20. The entrance of the bladder into the ileum.

Plate XXVIII.

Fig. 21. The distal portion of the ileum, cross-section.
Fig. 22. Cross-section of the colon; association of the Malpighian vessels with its walls. The ventral vessel is just coming in contact with the colon; the two vessels of the first series, with the common stem formed by their fusion, and the one vessel of the second series, with the common trunk formed by the fusion of all three, can still be seen. (A nerve separates the two vessels of the first series). The dorsal vessel is already joined to the colon, and the peritoneal sheath is beginning to extend out on each side.
Fig. 23. Cross-section of the colon; redivision of the trunks. The ventral vessel-trunk has just redivided into three vessels; the dorsal vessel-trunk has already redivided, and the vessels are beginning to migrate around the muscle fibres.
Fig. 24. Cross-section of colon: the migration of the vessels almost completed.
Fig. 25. Cross-section of colon: typical. Note the alternate arrangement of Malpighian vessels and longitudinal muscle fibres. (The upper "E" in this figure should be "C. M.")
Fig. 26. Cross-section of colon: the Malpighian vessels are increasing in size and tending to crowd the longitudinal muscles inside.

PLATE XXIX.

Fig. 27. Cross-section of colon: the Malpighian vessels have so increased in size as practically to surround the region; both longitudinal and circular muscles are much reduced.
Fig. 28. Cross-section of the rectum.
Fig. 29. A portion of the rectal epithelium, typical condition.
Fig. 30. A portion of the rectal epithelium, in the premolt condition.
Fig. 31. A portion of the rectal epithelium, just before a molt, the new intima forming.
Fig. 32. A cross-section through the rectal invagination.
Fig. 33. A cross-section through the invagination of the salivary gland.

ABBREVIATIONS USED IN THE FIGURES.

B.......Basement membrane.
BLA....Bladder.
BUC...Buccal cavity.
C^1......Primary cuticula.
C^2......Secondary cuticula.
CM....Circular muscles
D......Duct of salivary gland.
E.......Epithelium.
FORE..Fore-intestine.
H......Hypodermis.
HIND..Hind-intestine.
I^1.......Primary intima.
I^2.......Secondary intima.
I^3.......New intima, forming.
LM.....Longitudinal muscles.
M......Muscle.
MID...Mid-intestine.
N......Nerve.
O.......Oesophageal valve.
OE.....Oesophagus.
P.......Peritoneum.
PHA...Pharynx.
PM.....Pharyngeal muscle.
R.......Imaginal ring.
RC.....Replacement cell.
S.......Striated border.
SC.....Sarcolemma.
T.......Malpighian tube.